Surviving with a resident despot: do revegetated patches act as refuges from the effects of the noisy miner (*Manorina melanocephala*) in a highly fragmented landscape?

Alessio Mortelliti[1,2*], Karen Ikin[1], Ayesha Tulloch[1], Ross Cunningham[1], John Stein[1], Damian Michael[1], David B. Lindenmayer[1]

[1]Fenner School of Environment and Society, Australian Research Council Centre for Environmental Decisions, National Environmental Research Program, The Australian National University, Canberra, ACT 0200 (Australia).

[2]Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, 5755 Nutting Hall, Orono, ME (USA).

Running title: Surviving with a resident despot

Abstract

Aim. To provide, through a large-scale long-term field study, an empirical evaluation of the extent to which revegetated patches act as refuges for woodland bird species in the face of enhanced abundance of a native despotic species in a highly fragmented landscape.

Location. South-west slopes, New South Wales, Australia.

Methods. Birds were surveyed using point counts over a 9-year period. Colonization/extinction dynamics of local bird populations were modelled using multi-season occupancy models.

Results. We show how the spread of the noisy miner (*Manorina melanocephala*), an indirect effect of habitat loss and fragmentation, is now the main driver of bird distribution patterns, affecting 65% of the studied species, including 10 species of conservation concern. Noisy miners both increased the risk that birds would become extinct in patches and prevented birds colonizing new patches. We discovered that restoration plantings, despite having low noisy miner abundance, rarely acted as a refuge for bird species: only 6 out of 42 species, and only one of conservation concern, showed a positive response to plantings. Instead, bird species colonized or persisted more in regrowth or old growth sites where the abundance of the noisy miner was relatively low.

Main conclusions. Despite a major restoration effort of replanted vegetation over several decades, the majority of our target bird species preferred native woodland patches over plantings, and particularly native patches with a low abundance of the noisy miner. Our study showed that conservation actions such as habitat restoration aimed at reversing the effects of habitat loss and fragmentation should be preceded by a careful threat-mitigation prioritization considering, in particular, the indirect effects of fragmentation, such as the impact of despotic or invasive species. Our results support calls to manage noisy miners by undertaking actions that will reduce their numbers, such as through culling.

Introduction

Habitat loss and fragmentation due to the conversion of natural systems to cropland and pastures (Millennium Ecosystem Assessment, 2005;Fahrig, 2003) are major drivers of global change that may lead to non-reversible changes to populations, communities and interspecific interactions (Fahrig, 2003; Magrach et al., 2014; Pimm et al., 2014). Given that cropland and pastures currently cover 35% of the terrestrial land surface, and that by 2050 humans need to double food production (Foley et al., 2007, 2011), it is clear that biodiversity and humans will have to coexist on an increasingly fragmented planet.

The processes of habitat loss and habitat fragmentation act like a disease that debilitates an organism, exposing it, and potentially weakening its resilience, to additional diseases (i.e. like an immunodeficiency disorder, Chapin et al., 1997; Suding et al., 2004; Galetti et al., 2013). Likewise, these processes bring indirect effects, such as the spread of invasive species, which further threaten the viability of populations (Lindenmayer & Fischer, 2006; Didham et al., 2007; Brook et al., 2008).

The major approach to treating the 'disease' of habitat fragmentation is the restoration of native habitats through replanting vegetation (Clewell & Aronson, 2007). The effectiveness of habitat restoration has received considerable attention, particularly in recent years (Clewell & Aronson, 2007; Menz et al., 2013; Wortley et al., 2013). Yet, few studies have investigated what happens when we focus on the treatment of the perceived ultimate cause (i.e. restoring habitat to 'cure' fragmentation) while ignoring indirect effects of fragmentation (e.g. invasive species, changed fire regimes (Auerbach et al., 2015). The overarching goal of our study is therefore to provide, through a large-scale long-term field study, an empirical evaluation of what happens when highly fragmented landscapes undergo extensive restoration efforts but key indirect effects of fragmentation are not addressed.

Although revegetation efforts may sometimes involve extremely large investments (Clewell & Aronson, 2007; Smith, 2008; Atyeo & Thackway, 2009; Menz et al., 2013), even the most ambitious revegetation programs worldwide cannot fully restore native vegetation cover in highly fragmented landscapes. Realistically, revegetation programs aim at 'partially defragmenting' highly fragmented landscapes, such as increasing connectivity by establishing habitat corridors or increasing remnant native vegetation cover from, for example, 5% to 15% in a 20 year period (Thomson et al., 2009). Furthermore, although there is an increasing awareness of multiple threats and interactions between threats (Burgman et al., 2007; Didham et al., 2007; Doherty et al., 2015; Essl et al., 2015), revegetation programs typically do not explicitly account for the cumulative impacts of multiple threats. Indeed revegetation programs are often conducted under the implicit assumption that a

single action of revegetation will not only reverse the ultimate causes of species declines (habitat loss and fragmentation), but may also help to control the indirect effects of those threats (see Auerbach et al., 2014; Brown et al., 2014 for a discussion on multiple threats). The consequences of focusing on either the wrong threat, or a threat that has synergies with other processes in the landscape, are misspent conservation funds; thus revegetation programs may fail to prevent local species extinctions if the drivers of decline have not been addressed (Tulloch et al., 2015).

The loss and alteration of native eucalyptus woodland in Australia have caused the widespread increase of the noisy miner (*Manorina melanocephala*; Fig. S1, Maron et al., 2013). This is an aggressive and despotic native bird species, known to negatively affect whole bird assemblages over subcontinental scales by competitively excluding other bird species from woodland patches (Mac Nally et al., 2012; Maron et al., 2013; Thomson et al., 2015). The widespread increase of populations of the noisy miner has been unequivocally linked to the loss, fragmentation and degradation of native woodland habitats (Piper & Catterall, 2003; Oldland et al., 2009; Maron et al., 2013), and may thus be considered an indirect effect of habitat fragmentation. The aggressive exclusion of birds from potential woodland and forest habitat by over-abundant noisy miners is now listed as a 'key threatening process' by the Australian Government. Listing advice states that: '*measures available to reduce the negative impacts of noisy miners*' [include] '*habitat alteration to increase the size and structural complexity of habitat patches to make them less accessible to noisy miners while providing appropriate habitat for other native bird species. Such measures include revegetation, to increase the size and/or connectedness of patches or to increase density of the shrub layer within patches, removal of grazing or reducing fire frequency* (Threatened Species Scientific Committee, 2013). Thus, in addition to direct control, revegetation programs are explicitly advocated to create possible "refuges" for smaller birds (which are most vulnerable to the noisy miner; Piper & Catterall, 2003; Thomson et al., 2015). We emphasise that by "refuge" we mean areas with low abundance or absence of noisy miners where smaller bird species may be able to feed and reproduce without being subject to aggression from the noisy miners.

Our study was implemented in the south-west slopes region of eastern Australia which is equivalent in size to the country of Austria (80,000 Km^2). More than 85% of the native vegetation in the south-west slopes region has been cleared in the last 230 years (Benson, 2008). During the period 1990-2000, the area was subject to extensive region-wide revegetation efforts, often doubling the extent of wooded vegetation cover, resulting in increases of up to thousands of hectares of planted vegetation. Possibly due to limited awareness of the threat of the noisy miner at that time (Grey et al., 1997, 1998) [noisy miner effects were listed as a key threatening process only in 2014], no conservation action was planned in addition to revegetation. The scale of the

revegetation program thus provides a unique and unprecedented opportunity to evaluate the effects of revegetation on native bird species in an area characterised by strong negative effects of the noisy miner (Montague-Drake et al., 2011). In line with existing literature (Maron et al., 2013; Thomson et al., 2015), we expected that the noisy miner would exert a strong negative influence on the long-term population dynamics of other bird species. However, we also predicted that the extensive amount of revegetation in the region would provide a refuge for bird species and would thus help to buffer against the negative impact of the despotic noisy miner.

Methods

Study Area

Our study was conducted in the south-west slopes region of New South Wales (Fig. 1) is bordered by the following towns: Junee (0552952 E 6140128 N), Gundagai (600532 E 6119073 N), Albury (0494981 E 6008873 N) and Howlong (467090 E 6017897 N). It is characterised by hot summers and relatively cool winters (temperate climate). The native vegetation of the area is dominated by White Box *Eucalyptus albens*, Grey Box *E. microcarpa*, Yellow Box *E. melliodora*, and Blakely's Red Gum *E. blakelyi* (Benson, 2008). This woodland community occurs in remnant old growth patches and areas of natural regrowth (i.e. following land abandonment).

Starting in the 1960s, but mainly in the period 1990-2000, the south-west slopes area was subject to extensive revegetation programs managed by multiple stakeholders, including local government and environmental NGOs. Although an official repository of the extent and location of plantings does not exist, our estimates from LANDSAT imagery (see section below) suggest an average increase in woodland vegetation cover corresponding to 3-4% of the landscape (i.e. increases of 300-400 ha of vegetation in landscapes sized 10000 ha). Observations from local stakeholders are in line with these figures and suggest that occasionally increases of up to 10% of woodland cover (in 10000 ha areas) have occurred (Kylie Durant, pers. comm.). All plantings are fenced and are characterized by dense understory cover (0-53% cover; Lindenmayer et al., 2012) and *Eucalyptus* and *Acacia* midstory cover (0-37% *Acacia* cover and 0-73% *Eucalyptus* cover; Lindenmayer et al., 2010). More details on the study area are provided in Cunningham et al., 2008, 2014 and Lindenmayer et al., 2012. All plantings were at least 7 years old at the start of this study in 2000 and >15 were 10–20 years old (Lindenmayer et al., 2012).

Experimental design

The goal of our experimental design was to allow us to sample the long-term trajectories of bird populations in *old growth*, *regrowth* and *planting* woodland patches in the south-west slopes area.

We stratified our design to: 1) account for variation in vegetation cover and planting intensity (land cover), including areas with high vs low remnant vegetation cover and high vs low planting intensity, and 2) reduce the risk for spatial bias (i.e. clustering of specific patch types). Details on the design are provided by Cunningham et al. (2007) and in Appendix S1. In brief: our sampling was distributed over 46 farms, of which 27 had plantings. On each farm, we selected four to six sites (where possible) belonging to the three patch types (old growth, regrowth planting). Our final sample included 202 sites: 72 old growth patches, 66 regrowth patches, and 64 plantings.

The initial abundance of the noisy miner at the outset of this investigation was comparable in old growth and regrowth patches and was very low in plantings (Fig.S2). Thus, although we acknowledge this was fortuitous, it was ideal for the purposes of this investigation and did not confound our experimental design.

Bird surveys

We surveyed each site six times per year within a four day period. Surveys were conducted in the spring of the following years: 2002, 2004, 2006, 2008, 2009 and 2011, thus each patch was visited a total of 36 times between 2002 and 2011 Surveys were completed during early November, which is the breeding season for the majority of species and when summer migrants had arrived.

Each survey consisted of a five-minute point count; we recorded all birds seen or heard in a 50 m radius, but did not include birds flying over the site. Each point count was located on a 200 m transect (at 0, 100 m and 200 m points). Surveys were conducted by two observers: the first three by one observer on the same day, whereas the last three point counts were conducted by a different observer on a second day. We completed surveys within four hours from dawn and made sure we did not undertake surveys on days of bad weather (e.g. rainy or windy days). Bird surveys were conducted by the same group of experienced field technicians from The Australian National University throughout the duration of the 9 year study.

Data analysis

Predictor variables

Predictor variables included in the modelling phases (detailed below) were: 1) *tree cover*, which was measured with LANDSAT images (as detailed below) in a 78.5 ha circle; the size of the circle was chosen following Cunningham et al.(2014); 2) *increase in tree cover,* net increase in tree cover in the time-period since the previous survey; 3) *mean topographic wetness index* (TWI) an index of relative position in the landscape used as a proxy for site productivity (Montague-Drake et al., 2011;

171 Ikin et al., 2015); 4) *patch type* (categorical: old growth vs regrowth vs plantings) and 5) *year*
172 (categorical and continuous).
173
174 Tree Cover
175 For each year of bird survey, we calculated percent tree cover in a circle with a radius of 500 m
176 surrounding each site (equivalent to 78.5 ha). Source data were the time series grids of Forest Extent
177 and Change (version 9), produced by the Australian Government Department of Environment
178 (National Carbon Accounting System, http://pandora.nla.gov.au/pan/102841/20090728-
179 0000/www.climatechange.gov.au/ncas/reports/tech09.html). Landsat satellite imagery was used to
180 discriminate between forest and non-forest cover at a grid resolution of 25 m. Forest allocation to a
181 grid cell occurred where there was cell occupancy of at least 20 % of vegetation with potential to
182 reach 2 m high, over a minimum area of 0.2 ha.
183
184 Noisy miner abundance
185 For each year, noisy miner abundance was estimated during the point count surveys. Compared to
186 many other species, the noisy miner is very easy to detect and we considered our data reliable not
187 only for presence/absence surveys but also for abundance estimation (Cunningham et al., 1999;
188 Cunningham & Olsen, 2008; Mortelliti et al., 2015). We used the maximum number of individuals of
189 the noisy miner observed during the six visits (i.e. within a four day period) as a proxy for abundance
190 of this species at a given site.
191 We modelled noisy miner abundance by fitting Generalized Linear Mixed Effects Models
192 (GLMMs) with a Poisson distribution (logarithmic link; (Zuur et al., 2009) on the time-series of
193 abundance. Predictor variables for GLMMs included tree cover, TWI, patch type and year
194 (continuous); we used site as a random effect to account for repeated surveys.
195
196 Occupancy models
197 To account for imperfection in species detection, we fitted multiple season occupancy models
198 (MacKenzie et al., 2003). In addition to tackling the issue of false absences, multiple season
199 occupancy models allow the estimation of the turnover (colonization and extinction probability) of
200 local populations. Details of the protocol followed to fit occupancy models are provided in Appendix
201 S2. Each of the six point counts was defined as a *visit* to the site, thus each site was visited a total of
202 36 times (6 per year) between 2002 and 2011 (more details in Appendix 2).
203 Prior to occupancy analyses, we selected species with >1% detection rate (number of
204 detections/number of visits) which resulted in a selection of 53 species (including the noisy miner).

Following Burnham & Anderson (2002), we report models within 2 ΔAIC. Model predictions were based on model averaging and goodness of fit was measured using *Nagelkerke's* R^2 (Nagelkerke, 2004). We elected to focus our inference on species with a top ranking model showing a coefficient of determination of $R^2>0.15$, which resulted in a final set of 43 species (including the noisy miner).

Our final set of species included 13 species of conservation concern that are listed as 'threatened' under the *Threatened Species Conservation Act 1995* (New South Wales) or experienced a significant decline in reporting rate within the south-west slopes bioregion (Barrett et al., 2003). Conservation status is specified in Table 2. We acknowledge that these 13 species are the most common of the 33 species of conservation concern present in the area as we were not able to include rarer species, such as the flame robin (*Petroica phoenicea*) and the gang-gang cockatoo (*Callocephalon fimbriatum*).

Results

Noisy miner abundance

By fitting GLMMs to time-series data, we found that noisy miner abundance (mean=2.2 individuals, range= 0-26) was significantly higher in more productive sites and significantly lower in plantings than in regrowth and old growth sites (Table 1, Fig. S2). Furthermore, we found evidence for a decrease in abundance through time. Occupancy models for the noisy miner mirrored the results of the GLMMs, showing a decrease in colonization probability with time and higher extinction risk (and lower probability of being occupied during the first season) in plantings compared to other patch types (Table 2).

Occupancy models

A full list of the top ranking multiple-season occupancy models (within 2 ΔAIC) is provided in Table 2. Model fit was relatively high (average coefficient of determination: $R^2=0.35$, range of R^2 values = 0.15-0.71).

To simplify interpretation of the results, we grouped species according to their response to predictor variables (Mortelliti & Lindenmayer, 2015). A negative response implied either a decrease in colonization and/or an increase in extinction, or low probability of a site being occupied in the first season in response to a given predictor variable, whereas a positive response implied either an increase in colonization and/or a decrease in extinction, or higher probability of a site being occupied in the first season. An overview of results is provided in Fig. 2 and Table S1. We found that 65% of the species (28 out of 42, including 10 species of conservation concern) were negatively affected by increasing noisy miner abundance (Fig. 2; an example of model predictions is provided in

239 Fig. 3). All were of smaller or equivalent body mass to the noisy miner. When noisy miner abundance
240 was high, 24 species had lower colonization rates and 10 species had higher extinction rates (six
241 species had both decreased colonization and increased extinction). Likewise, 11 species had a lower
242 probability of occupying a site in the first season with higher noisy miner abundance. We also found
243 that seven species were positively associated with the noisy miner.
244 We found that for 20 species (47%, including nine species of conservation concern), colonization
245 rates were lower in plantings compared to the other two patch types and/or extinction rates were
246 higher in plantings. Fourteen of these species also were negatively affected by the noisy miner.
247 Model predictions for these species showed that: (1) the magnitude of the effect of the noisy miner
248 was particularly strong compared to the effects of patch type, and (2) in cases with high abundance
249 of the noisy miner, the colonization rate for an old growth patch was comparable to that of a
250 planting with no noisy miners (Fig. 3a and b). Conversely, we found that only six species (including
251 one species of conservation concern [the yellow-rumped thornbill]), had colonization rates higher in
252 plantings than in the other types of patches.
253 Twenty bird species responded positively to nearby tree cover whereas three species responded
254 negatively (the brown songlark, the common starling and the crested pigeon). These are all open
255 country species that live in woodland but forage in open areas.
256 Twelve of the species responding positively to tree cover also were negatively affected by the
257 noisy miner. Model predictions for these species (examples in Fig 3) showed that 1) the magnitude
258 of the effect of the noisy miner was particularly strong compared to the effects of tree cover, and 2)
259 in cases with very high abundance of the noisy miner, the colonization rate remained close to zero
260 even with relatively large values of tree cover (Fig. 3c and d).
261 We found that only three species responded to the increase in vegetation cover within the study
262 period: one positively (the common bronzewing, a woodland species) and two negatively (the red
263 rumped parrot and the willie wagtail, both open country species).
264 We found that patterns of detectability varied between species. The categorical year variable
265 was the main factor affecting detectability in 29 species (Table 2). According to this model,
266 detectability varied in each of the sampling years (an example is provided in Fig. S3). The numerical
267 year variable was the main factor affecting detectability in eight species. For four of these species,
268 we found that detectability increased through the years whereas in four cases the trend was
269 negative. The remaining six species had a constant detection probability.
270

Discussion

Through our large-scale and long-term field study, we show how the abundance of the noisy miner, an indirect effect of habitat loss and fragmentation, is now the main driver of bird distribution patterns in the highly fragmented south-west slopes region of Australia. Using occupancy models to explain the mechanisms of bird population change in this fragmented landscape revealed that the main effect of the noisy miner was to prevent bird colonization of unoccupied sites and to increase extinction risk in occupied sites. We found that despite the low abundance or absence of noisy miners (Table 1 and Fig. S2), plantings did not act as a refuge for nine out of ten common species of conservation concern. Rather, bird species colonize regrowth or old growth sites where the abundance of the noisy miner is relatively low, and tend to avoid plantings in the same way that noisy miners do. Our findings highlight that reversing the negative effects of habitat loss and fragmentation requires a careful prioritization of actions and the concurrent treatment of both direct and indirect effects (Auerbach et al., 2015).

Biological interpretation of models

The negative effects of the noisy miner in the south-west slopes area is consistent with existing knowledge. In the southern part of its distribution, this species is associated with woodland edges and/or patches less than 36 ha (Clarke & Oldland, 2007), which in highly fragmented landscapes (<15% tree cover) correspond to most woodland areas. Also consistent with previous studies that have shown that the noisy miner is particularly successful at excluding smaller-sized birds (Maron et al., 2013; Thomson et al., 2015), we found that most (75%) 'noisy miner-sensitive' species were smaller (e.g. the yellow thornbill, the superb fairy-wren and the red-capped robin) and the remaining 25% were approximately the same size (e.g. the grey shrike-thrush and the little friarbird; Table 2). Likewise, in line with Maron et al. (2013), we found that several species such as the Australian magpie and the grey butcherbird responded positively to the abundance of the noisy miner. According to Maron & Kennedy (2007) and Thomson et al. (2015), domination of sites by the noisy miner is associated with an increase in the density of predatory and larger bird species. These species may further exacerbate the impact of the noisy miner and they are also known to cooperate with the noisy miner in antipredator responses (Maron, 2009).

We contributed to existing knowledge on noisy miner impacts by providing empirical evidence that this species is interfering with long term spatial population dynamics (i.e. colonization/extinction) of other birds. Specifically, our findings show how noisy miners prevent species from establishing a population in unoccupied patches, which may also negatively affect individual dispersal and the connectivity between remnant populations. Furthermore, we show how

noisy miner presence may lead to the local extinction of other species. The balance of colonization/extinction dynamics is fundamental for the long-term persistence of spatially structured populations in highly fragmented landscapes (Hanski & Gaggiotti, 2004). The interference of noisy miners with the dynamics of spatially structured populations may thus have an effect beyond the single patch to have an impact at broader landscape scales. Hence, our findings are of high importance and underscore the spatial and temporal pervasiveness of the impact of the noisy miner.

Previous studies suggest that the suitability of plantings for the noisy miner may depend on the dominant tree species and on the density of understory shrubs (Hastings & Beattie, 2006; Maron, 2007). We found that the probability of occupancy and the local abundance of the noisy miner were significantly lower in plantings than in other patch types, potentially because the plantings had particularly high understory cover compared to the remnant patches (Lindenmayer et al., 2010, 2012). Surprisingly, however, plantings did not appear to act as refuges for bird species. This is despite listing advice suggesting that increasing the density of the shrub layer might abate the threat of noisy miners (Threatened Species Scientific Committee, 2013). Our findings therefore provide two implications for management. First, we provide empirical evidence of the lower performance of plantings in supporting long-term bird population dynamics compared to other patch types. Second, we provide strong evidence in support for the need to address the indirect effects of fragmentation (such as the impact of the despotic noisy miner) in synergy with restoration (Brook et al., 2008). For at least 14 species (including eight species of conservation concern), we found evidence that bird species were avoiding plantings and selecting old growth /regrowth patches where the abundance of noisy miners was low. In such cases, the priority conservation strategy should be to decrease the abundance of the noisy miner. Indeed we suggest that future studies should focus on evaluating the efficacy of culling (Clarke & Grey, 2010).

Our predictions shown in Fig. 3 suggest that for many native bird species, a small increase in noisy miner abundance within a patch may lead to a considerable decrease in colonization or increase in extinction probability. This suggests that the effect of the noisy miner is particularly strong even when their abundance is not particularly high (see also Thomson et al., 2015). Consistent with previous studies (Montague-Drake et al., 2009; Thomson et al., 2015), we show that productivity positively affected the local abundance of the noisy miner, which implies that other bird species may be relegated to less productive areas. Most importantly, our results show that management actions to decrease the abundance of the noisy miner (e.g. through culling) should be targeted towards the most productive areas of the landscapes, where the impact of noisy miners may be higher.

The relative ineffectiveness of plantings that we have observed is partly consistent with existing knowledge (Brawn, 2006; Munro et al., 2007; Mac Nally et al., 2010). Outcomes of previous studies on plantings have been highly variable, ranging from a negative to positive effect of plantings on birds depending on the population parameter considered. Plantings may support species-rich communities (Munro et al., 2007) and breeding success in restored areas can be comparable with breeding success in areas of remnant native vegetation (Brawn, 2006; Small et al., 2007). However, other studies have suggested that plantings may benefit only the most generalist species in bird communities (Mac Nally *et al.* 2010) or may be less effective than remnants for bird breeding performance (Larison et al., 2001; Barrett et al., 2008; Selwood et al., 2009). From the perspective of long-term colonization/extinction dynamics that we have examined, our results suggest a 'non-positive' effect of plantings compared to other patch types. We emphasise that this does not mean that the effect is 'negative'. Rather, we show that plantings do not substitute the ecological value of remnant vegetation and should not be used to offset the destruction of existing vegetation. Indeed, our results show that bird species use plantings and six species even colonize or persist more in plantings than other patch types (the rufous whistler, red wattlebird, superb fairy wren, buff-rumped thornbill, yellow thornbill, and the yellow-rumped thornbill, which is a species of conservation-concern Table S1).

Finally, we did not consider variables such as the shape, structure, and age context of plantings which are known to play an important role in affecting the response of bird species to plantings (Munro *et al.* 2007; Gardali *et al.* 2006; Barrett *et al.* 2008; Lindenmayer *et al.* 2012). Indeed, it is likely that in the longer term, plantings will increase in suitability and thus may be more valuable to long-term population dynamics. For this reason, we emphasise that we are not suggesting that restoration efforts in highly fragmented landscapes be diminished. Rather, our findings emphasize that: 1) plantings may not be used to offset habitat loss and degradation and 2) habitat restoration should be preceded by a careful threat-mitigation prioritization considering, in particular, the indirect effects of fragmentation, such as the impact of despotic or invasive species.

We also acknowledge that we were not able to include measurements of the structure or quality of different patches which may have a strong effect on the noisy miner (Montague-Drake et al., 2011). Likewise, we acknowledge that although our study was focused on two key-population-level parameters (local extinction and colonization), future studies focusing on more detailed dynamics of the populations, such as fluctuations in abundance and reproductive performance, will provide further understanding on the mechanisms involved in determining the observed responses to noisy miners (Mortelliti et al., 2014).

Implications for conservation

In our study system, a despotic native species which has increased as a consequence of habitat loss and degradation has now become the major force shaping the distribution of the remaining bird species. Despite a substantial restoration effort encompassing >2000 ha of replanted vegetation over several decades, the majority of bird species (including nine of 13 species of conservation concern) tended to colonize and persist more in old growth and regrowth patch types rather than in plantings, particularly where the abundance of noisy miners was low. We foresee two major implications of our study:

1) *Plantings do not act as refuges*. Contrary to our predictions, plantings were not acting as refuges for bird species and were not as effective as existing vegetation types in supporting long-term spatial population dynamics of bird species. **Thus, plantings should not be used as a justification for offsetting (i.e. counterbalancing) vegetation clearing.**

2) *Restoration efforts must be undertaken in synergy with the treatment of the indirect effects of fragmentation.* Our study shows that conservation actions such as habitat restoration, which aim at reversing the effects of habitat loss and fragmentation, should be anticipated by a careful prioritization considering, in particular, the indirect effects of fragmentation (see Tulloch et al., 2015). We provided compelling empirical evidence that a synergistic treatment of ultimate causes and of the indirect effects is fundamental and will surely maximise the chances of success (Auerbach et al., 2014). **In our study system, the priority is to manage noisy miners by undertaking actions that will reduce their abundance such as culling** (i.e. targeted, at least at initial stages, towards old growth and regrowth patches located in the most productive parts of the landscape). This finding is congruent with resilience theory (Walker & Salt, 2012), and supports the tenet that "the way back is not the same as the way there": reversing the negative effects of humans on complex ecological systems such as woodland ecosystems is not straightforward; however, efforts to deal explicitly with this complexity will surely prove rewarding.

Acknowledgements

Thanks Dean Ansell, Shana Nurenberg, Kylie Durant and David Salt for valuable conversations on plantings and resilience. Thanks to ANU field staff for long-term support in the project, thanks to land-owners for allowing access to field sites and thanks to Claire Foster for feedback on the manuscript. Thanks to Dr. Alan Andersen and three anonymous reviewers for their constructive feedback on the manuscript

406 **References**

407 Atyeo, C. & Thackway, R. (2009) Mapping and monitoring revegetation activities in Australia –
408 towards national core attributes. *Australasian Journal of Environmental Management*, **16**, 140–
409 148.

410 Auerbach, N., Tulloch, A.I.T., & Possingham H.P. (2014) Informed actions: where to cost effectively
411 manage multiple threats to species to maximize return on investment. *Ecological Applications*,
412 **24**, 1357–1373.

413 Auerbach, N., Wilson, K., Tulloch, A.I.T., Rhodes, J.R., & Possingham, H.P. (2015) Accounting for
414 interactions and spatial dependence in threat management alters conservation priorities.
415 *Conservation Biology*, **29**, 1626-1635.

416 Barrett, G., Freudenberger, D., Drew, A., Stol, J., Nicholls, A., & Cawsey E. (2008) Colonisation of
417 native tree and shrub plantings by woodland birds in an agricultural landscape. *Wildlife*
418 *Research*, **35**, 19–32.

419 Barrett, G., Silcocks, A., Barry, S., Cunningham, R., & Poulter, R. (2003) *The new atlas of Australian*
420 *birds.* Royal Australasian Ornithologists Union., Hawthorn East.

421 Benson, J. (2008) New South Wales vegetation classification and assessment: Part 2 plant
422 communities of the NSW Southwestern Slopes Bioregion and update of NSW Western Plains
423 plant communities, Version 2 of the NSWVCA database. *Cunninghamia*, **104**, 599–673.

424 Brawn, J.D. (2006) Effects of Restoring Oak Savannas on Bird Communities and Populations.
425 *Conservation Biology*, **20**, 460–469.

426 Brook, B.W., Sodhi, N.S., & Bradshaw, C.J. (2008) Synergies among extinction drivers under global
427 change. *Trends in ecology & evolution*, **23**, 453–60.

428 Brown, C.J., Saunders, M.I., Possingham, H.P., & Richardson, A.J. (2014) Interactions between global
429 and local stressors of ecosystems determine management effectiveness in cumulative impact
430 mapping. *Diversity and Distributions*, **20**, 538–546.

431 Burgman, M., Keith, D., Hopper, S., Widyatmoko, D., & Drill, C. (2007) Threat syndromes and
432 conservation of the Australian flora. *Biological Conservation*, **134**, 73–82.

433 Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical*
434 *Information-Theoretic Approach.* Springer-Verlag,

435 Chapin, F., Walker, B., & Hobbs, R. (1997) Biotic control over the functioning of ecosystems. *Science*,
436 **277**, 500–503.

437 Clarke, M. & Grey, M. (2010) Managing an over-abundant native bird: the noisy miner (Manorina
438 macrocephala). *Temperate woodland conservation and management* (ed. by D. Lindenmayer,
439 A. Bennett, and R. Hobbs), pp. 115–126. CSIRO Publishing, Collingwood.

440 Clarke, M.F. & Oldland, J.M. (2007) Penetration of remnant edges by noisy miners (Manorina
441 melanocephala) and implications for habitat restoration. *Wildlife Research*, **34**, 253.

Clewell, A. & Aronson, J. (2007) *Ecological Restoration: Principles, Values, and Structure of an Emerging Profession.* Island Press, Washington,D.C.

Cunningham, R. & Olsen, P. (2008) A statistical methodology for tracking long-term change in reporting rates of birds from volunteer-collected presence–absence data. *Biodiversity and Conservation*, **18**, 1305–1327.

Cunningham, R.B., Lindenmayer, D.B., Crane, M., Michael, D., & MacGregor, C. (2007) Reptile and arboreal marsupial response to replanted vegetation in agricultural landscapes. *Ecological applications : a publication of the Ecological Society of America*, **17**, 609–19.

Cunningham R.B., Lindenmayer D.B., Crane M., Michael D., MacGregor C., Montague-Drake R., & Fischer J. (2008) The combined effects of remnant vegetation and tree planting on farmland birds. *Conservation Biology*, **22**, 742–752.

Cunningham, R.B., Lindenmayer, D.B., Crane, M., Michael, D.R., Barton, P.S., Gibbons, P., Okada, S., Ikin K., & Stein J. a. R. (2014) The law of diminishing returns: woodland birds respond to native vegetation cover at multiple spatial scales and over time. *Diversity and Distributions*, **20**, 59–71.

Cunningham, R.B., Lindenmayer, D.B., Nix, H.A., & Lindenmayer, B.D. (1999) Quantifying observer heterogeneity in bird counts. *Austral Ecology*, **24**, 270–277.

Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T. A, & Ewers, R.M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in ecology & evolution*, **22**, 489–96.

Doherty, T.S., Dickman, C.R., Nimmo, D.G., & Ritchie, E.G. (2015) Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation*, **190**, 60–68.

Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Pyšek, P., Wilson, J.R.U., & Richardson, D.M. (2015) Historical legacies accumulate to shape future biodiversity in an era of rapid global change. *Diversity and Distributions*, **5**, 534-547.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.

Foley, J. A, Monfreda, C., Ramankutty, N., & Zaks, D. (2007) Our share of the planetary pie. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 12585–6.

Foley, J. A, Ramankutty, N., Brauman, K. A, Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D., & Zaks, D.P.M. (2011) Solutions for a cultivated planet. *Nature*, **478**, 337–42.

Galetti, M., Guevara, R., Côrtes, M.C., Fadini, R., Von Matter, S., Leite, A.B., Labecca, F., Ribeiro, T., Carvalho, C.S., Collevatti, R.G., Pires, M.M., Guimarães, P.R., Brancalion, P.H., Ribeiro, M.C., & Jordano, P. (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, **340**, 1086–90.

480 Gardali, T., Holmes, A., & Small, S. (2006) Abundance patterns of landbirds in restored and remnant
481 riparian forests on the Sacramento River, California, USA. *Restoration Ecology*, **14**, 391–403.

482 Grey, M., Clarke, M., & Loyn, R. (1997) Initial changes in the avian communities of remnant eucalypt
483 woodlands following a reduction in the abundance of noisy miners, Manorina melanocephala.
484 *Wildlife Research*, **24**, .

485 Grey, M., Clarke, M., & Loyn, R. (1998) Influence of the Noisy Miner Manorina melanocephala on
486 avian diversity and abundance in remnant Grey Box woodland. *Pacific Conservation*, **4**, 55–69.

487 Hanski, I. & Gaggiotti, O.E. (2004) *Ecology, Genetics, and Evolution of Metapopulations.* Elsevier
488 Academic Press, Boston.

489 Hastings, B.R.A. & Beattie, A.J. (2006) Stop the bullying in the corridors: Can including shrubs make
490 your revegetation more Noisy Miner. *Ecological management and restoration* **7**, 105-112.

491 Ikin, K., Mortelliti, A., Stein, J., Michael, D., Crane, M., Okada, S., Wood, J., & Lindenmayer, D. (2015)
492 Woodland habitat structures are affected by both agricultural land management and abiotic
493 conditions. *Landscape Ecology*, **30**, 1387–1403.

494 Larison B., Laymon S., Williams P., & Smith T. (2001) Avian responses to restoration: nest-site
495 selection and reproductive success in Song Sparrows. *The Auk*, **118**, 432–442.

496 Lindenmayer, D. & Fischer, J. (2006) *Habitat Fragmentation and Landscape Change. An Ecological*
497 *and Conservation Synthesis.* Island Press, Washington.

498 Lindenmayer, D.B., Knight, E.J., Crane, M.J., Montague-Drake, R., Michael, D.R., & MacGregor, C.I.
499 (2010) What makes an effective restoration planting for woodland birds? *Biological*
500 *Conservation*, **143**, 289–301.

501 Lindenmayer, D.B., Northrop-Mackie, A.R., Montague-Drake, R., Crane, M., Michael, D., Okada, S., &
502 Gibbons, P. (2012) Not all kinds of revegetation are created equal: Revegetation type
503 influences bird assemblages in threatened australian woodland ecosystems. *PLoS ONE*, **7**,
504 e34527.

505 MacKenzie, D., Nichols, J., & Hines, J. (2003) Estimating site occupancy, colonization, and local
506 extinction when a species is detected imperfectly. *Ecology*, **84**, 2200–2207.

507 Magrach, A., Laurance, W.F., Larrinaga, A.R., & Santamaria, L. (2014) Meta-analysis of the effects of
508 forest fragmentation on interspecific interactions. *Conservation biology : the journal of the*
509 *Society for Conservation Biology*, **28**, 1342–8.

510 Maron, M. (2007) Threshold effect of eucalypt density on an aggressive avian competitor. *Biological*
511 *Conservation*, **136**, 100–107.

512 Maron, M. (2009) Nesting, foraging and aggression of Noisy Miners relative to road edges in an
513 extensive Queensland forest. *Emu*, **109**, 75.

514 Maron, M., Grey, M.J., Catterall, C.P., Major, R.E., Oliver, D.L., Clarke, M.F., Loyn, R.H., Mac Nally, R.,
515 Davidson, I., & Thomson, J.R. (2013) Avifaunal disarray due to a single despotic species.
516 *Diversity and Distributions*, **19**, 1468–1479.

517 Maron, M. & Kennedy, S. (2007) Roads, fire and aggressive competitors: Determinants of bird
518 distribution in subtropical production forests. *Forest Ecology and Management*, **240**, 24–31.

519 Menz, M., Dixon, K., & Hobbs, R. (2013) Hurdles and opportunities for landscape-scale restoration.
520 *Science*, **339**, 526–7.

521 Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Synthesis.* Island
522 Press, Washington DC.

523 Montague-Drake, R.M., Lindenmayer, D.B., & Cunningham, R.B. (2009) Factors affecting site
524 occupancy by woodland bird species of conservation concern. *Biological Conservation*, **142**,
525 2896–2903.

526 Montague-Drake, R.M., Lindenmayer, D.B., Cunningham, R.B., & Stein, J. A. (2011) A reverse
527 keystone species affects the landscape distribution of woodland avifauna: a case study using
528 the Noisy Miner (*Manorina melanocephala*) and other Australian birds. *Landscape Ecology*, **26**,
529 1383–1394.

530 Mortelliti, A., Westgate, M., Stein, J., Wood, J., & Lindenmayer, D.B. (2015) Ecological and spatial
531 drivers of population synchrony in bird assemblages. *Basic and Applied Ecology*, **16**, 269–278.

532 Mortelliti, A. & Lindenmayer, D.B. (2015) Effects of landscape transformation on bird colonization
533 and extinction patterns in a large-scale, long-term natural experiment. *Conservation Biology*,
534 **29**, 1314–1326.

535 Mortelliti, A., Sozio, G., Driscoll, D., Bani, L., Boitani, L., & Lindenmayer, D. (2014) Population and
536 individual-scale responses to patch size, isolation and quality in the hazel dormouse. *Ecosphere*,
537 **5**, 1–21.

538 Munro, N.T., Lindenmayer, D.B., & Fischer, J. (2007) Faunal response to revegetation in agricultural
539 areas of Australia: A review. *Ecological Management & Restoration*, **8**, 199–207.

540 Nagelkerke, N.J.D. (2004) A note on a general definition of the coefficient of determination.
541 *Biometrika*, **78**, 691–692.

542 Mac Nally, R., Bowen, M., Howes, A., McAlpine, C.A., & Maron, M. (2012) Despotic, high-impact
543 species and the subcontinental scale control of avian assemblage structure. *Ecology*, **93**, 668–
544 678.

545 Mac Nally, R., De Vries, L., & Thomson, J.R. (2010) Are Replanted Floodplain Forests in Southeastern
546 Australia Providing Bird Biodiversity Benefits? *Restoration Ecology*, **18**, 85–94.

547 Oldland, J.M., Taylor, R.S., & Clarke, M.F. (2009) Habitat preferences of the noisy miner (Manorina
548 melanocephala) - a propensity for prime real estate? *Austral Ecology*, **34**, 306–316.

549 Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts,
550 C.M., & Sexton, J.O. (2014) The biodiversity of species and their rates of extinction, distribution,
551 and protection. *Science*, **344**, 1246752.

552 Piper, S. & Catterall, C. (2003) A particular case and a general pattern: hyperaggressive behaviour by
553 one species may mediate avifaunal decreases in fragmented Australian forests. *Oikos*, **3**, 602–
554 614.

555 Selwood, K., Mac Nally, R., & Thomson, J.R. (2009) Native bird breeding in a chronosequence of
556 revegetated sites. *Oecologia*, **159**, 435–446.

557 Small S., III F.T., Geupel G., & Faaborg J. (2007) Spotted Towhee population dynamics in a riparian
558 restoration context. *The Condor*, **109**, 721–732.

559 Smith, F.P. (2008) Who's planting what, where and why – and who's paying? *Landscape and Urban*
560 *Planning*, **86**, 66–78.

561 Suding, K.N., Gross, K.L., & Houseman, G.R. (2004) Alternative states and positive feedbacks in
562 restoration ecology. *Trends in ecology & evolution*, **19**, 46–53.

563 Thomson, J., Moilanen, A., Vesk, P.A., Bennett, A.F., & Mac Nally, R. (2009) Where and when to
564 revegetate: a quantitative method for scheduling landscape reconstruction. *Ecological*
565 *Applications*, **19**, 817–828.

566 Thomson, J.R., Maron, M., Grey, M.J., Catterall, C.P., Major, R.E., Oliver, D.L., Clarke, M.F., Loyn, R.H.,
567 Davidson, I., Ingwersen, D., Robinson, D., Kutt, A., MacDonald, M. A., & Mac Nally, R. (2015)
568 Avifaunal disarray: quantifying models of the occurrence and ecological effects of a despotic
569 bird species. *Diversity and Distributions*, **21**, 451–464.

570 Threatened Species Scientific Committee (2013). Amendments to the List of Key Threatening
571 Processes. https://www.comlaw.gov.au/Details/F2015L00502

572 Tulloch, V.J., Tulloch, A.I., Visconti, P., Halpern, B.S., Watson, J.E., Evans, M.C., Auerbach, N. A,
573 Barnes, M., Beger, M., Chadès, I., Giakoumi, S., McDonald-Madden, E., Murray, N.J., Ringma, J.,
574 & Possingham, H.P. (2015) Why do we map threats? Linking threat mapping with actions to
575 make better conservation decisions. *Frontiers in Ecology and the Environment*, **13**, 91-99.

576 Walker, B. & Salt, D. (2012) *Resilience Practice.* Island Press, Washington.

577 Wortley, L., Hero, J.-M., & Howes, M. (2013) Evaluating Ecological Restoration Success: A Review of
578 the Literature. *Restoration Ecology*, **21**, 537–543.

579 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., & Smith, G.M. (2009) *Mixed effects models and*
580 *extensions in ecology with R.* Springer, New York.

581

582 **Supporting Information**

583 Additional Supporting Information may be found in the online version of this article:

584 **Appendix S1.** {Details on the criteria adopted for selecting sites}

585 **Appendix S1.** {Detailed methodology for the occupancy modelling}

586 **Figure S1** {Photo of the noisy miner *Manorina melanocephala*}

587 **Figure S2** {Abundance of the noisy miner during the first year of investigation}

588 **Table S1** {Summary of the relationships between occupancy models parameters and predictor
589 variables}
590

591 **Biosketch**

592 AM is an Assistant Professor at the University of Maine. His main research interest is the response of
593 mammals and birds to land-use change. Author contributions: AM designed this study, DBL and RC
594 designed the habitat restoration experiment. AM performed the analyses and wrote the paper, KI,
595 AT and DBL contributed to writing the paper, JS conducted the LANDSAT analyses.

596 Table 1. Model parameters predicting noisy miner abundance showing the parameter (β) and
597 standard error (SE) for each variable in the final model (N=1102 observations in 203 sites). Fitted
598 model: GLMM with a Poisson distribution with logarithmic link; variable significance was tested with
599 a Wald test. The variable PT (patch type) is a categorical variable, with 'old growth' as the reference
600 category; Year=number of years since the beginning of the study; TWI = position in the landscape
601 (productivity) index; TC= logarithm of tree cover (in ha) in the 78.5 ha circle surrounding each site.
602 All continuous variables were scaled.
603

Term			Wald's test	significance
Random effects	Variance	Standard Deviation		
Site	1.74	1.31		
Fixed effects	β	SE	*z*	*p*
Intercept	115.81	13.89	8.33	*<0.001*
Year	-0.05	0.01	-8.28	*<0.001*
TWI	0.32	0.10	3.16	*=0.001*
PT (planting)	-1.61	0.25	-6.20	*<0.001*
PT (regrowth)	-0.25	0.23	-1.06	*0.28*
TC	-0.02	0.01	-1.74	*0.08*

604

Table 2. Top ranked occupancy models. Model ranking according to ΔAIC (delta Akaike Information Criterion); only models <2 are shown. Ψ= probability of a site being occupied during the first survey, ϒ=probability of colonization; ε=probability of extinction, p=detection probability; PT= patch type (plantings, vs regrowth vs old growth); TC=tree cover in the 78.5 ha circle, Y=year (categorical covariate); YN=year (numeric covariate); *=including spatial autocovariate; R^2 = Nagelkerke's coefficient of determination; (.)= constant model (no covariate). Species underlined are species of conservation concern.

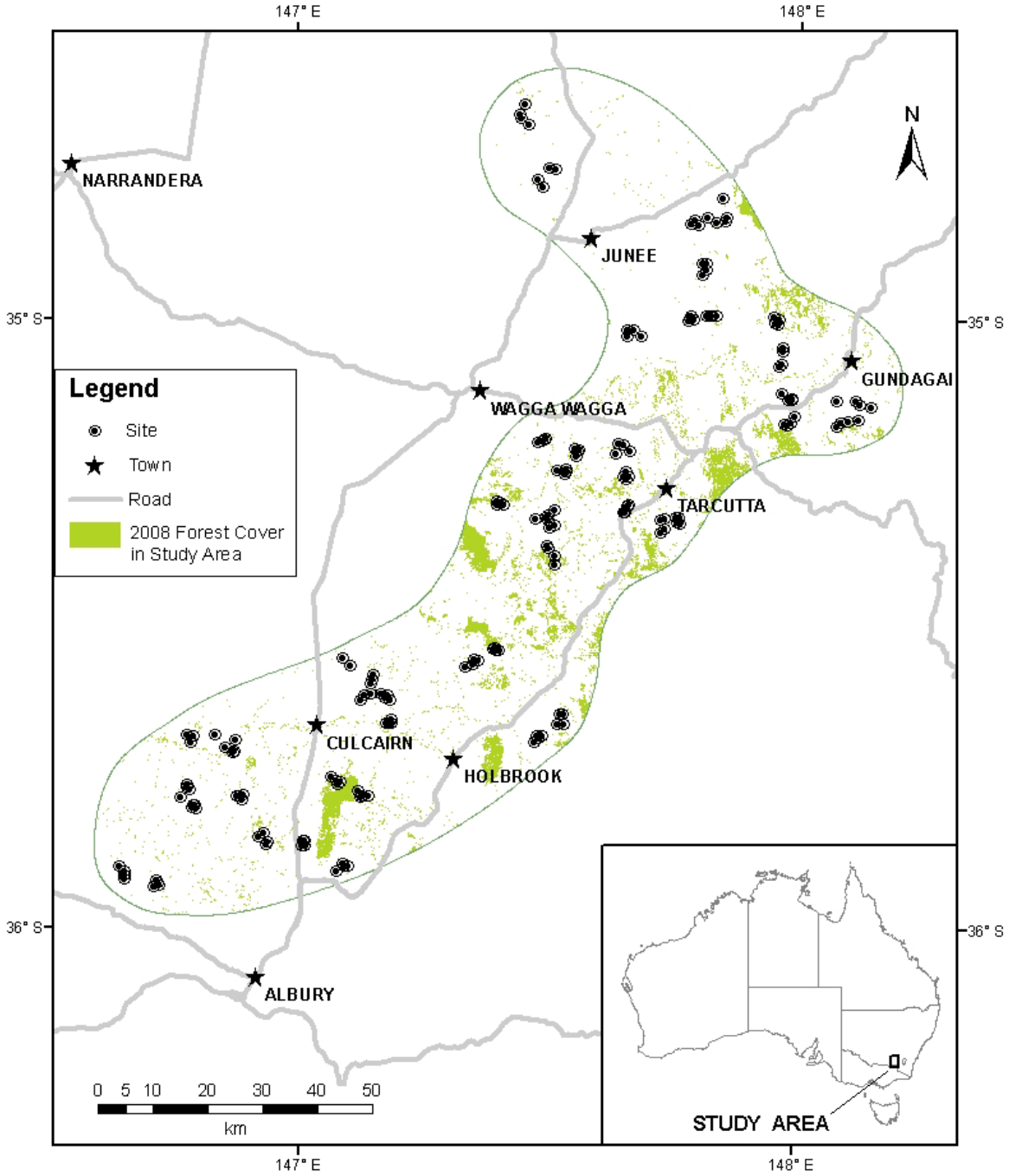
Species	**Scientific name**	**Model**	**ΔAIC**	***R²***
Australian magpie	*Cracticus tibicen*	Ψ(NM)ϒ(.)ε(TC+NM)p(Y)	0.000	0.191
		Ψ(NM)ϒ(TC+NM)ε(TC+NM)p(Y)	1.298	0.201
		Ψ(NM)ϒ(YN)ε(TC+NM)p(Y)	1.857	0.191
Black-faced cuckoo-shrike	*Coracina novaehollandiae*	Ψ(.)ϒ(PT+NM)ε(PT+NM)p(.)	0.000	0.309
Brown songlark	*Cincloramphus cruralis*	Ψ(TC)ϒ(TC+NM)ε(YN)p(Y)	0.000	0.598
Brown treecreeper	*Climacteris picumnus*	Ψ(TC)ϒ(PT+NM)ε(PT+NM)p(.)	0.000	0.294
Buff-rumped thornbill	*Acanthiza reguloides*	Ψ(.)ϒ(PT)ε(TC)p(YN)	0.000	0.241
		Ψ(.)ϒ(PT)ε(TC+NM)p(YN)	0.272	0.247
		Ψ(.)ϒ(TC+NM)ε(.)p(YN)	1.580	0.227
Cockatiel	*Nymphicus hollandicus*	Ψ(.)ϒ(TC+NM)ε(TC+NM)p(Y)	0.000	0.519
		Ψ(.)ϒ(TC+NM)ε(.)p(Y)	1.519	0.505
		Ψ(.)ϒ(ITC+NM)ε(ITC)p(Y)	1.551	0.515
Common bronzewing	*Phaps chalcoptera*	Ψ(TC)ϒ(.)ε(ITC+TC)p(Y)	0.000	0.274
		Ψ(TC)ϒ(TC)ε(ITC+TC)p(Y)	0.571	0.280
		Ψ(TC)ϒ(ITC)ε(ITC+TC)p(Y)	1.110	0.278
Common starling	*Sturnus vulgaris*	Ψ(TC)ϒ(TC+NM)ε(PT)p(Y)	0.000	0.442
		Ψ(TC)ϒ(TC)ε(PT)p(Y)	0.743	0.434
Crested pigeon	*Ocyphaps lophotes*	Ψ(TC)ϒ(TC)ε(NM)p(Y)	0.000	0.363
Crested shrike-tit	*Falcunculus frontatus*	Ψ(NM)ϒ(TC+NM)ε(PT)p(Y)	0.000	0.404
Diamond firetail	*Stagonopleura guttata*	Ψ(NM)ϒ(PT+NM)ε(.)p(YN)	0.000	0.283
Dusky woodswallow	*Artamus cyanopterus*	Ψ(TC)ϒ(TC+NM)ε(PT)p(.)	0.000	0.296
Eastern rosella*	*Platycercus eximius*	Ψ(NM)ϒ(YN)ε(PT+NM)p(YN)	0.000	0.456
Fuscous honeyeater	*Lichenostomus fuscus*	Ψ(TC)ϒ(NM)ε(TC)p(YN)	0.000	0.366
		Ψ(TC)ϒ(PT+NM)ε(.)p(YN)	0.750	0.370
		Ψ(TC)ϒ(TC+NM)ε(TC+NM)p(YN)	0.834	0.377
		Ψ(TC)ϒ(TC+NM)ε(.)p(YN)	1.962	0.359
Galah	*Eolophus roseicapillus*	Ψ(PT)ϒ(PT)ε(TC+NM)p(Y)	0.000	0.413
Grey butcherbird*	*Cracticus torquatus*	Ψ(NM)ϒ(TC+NM)ε(TC+NM)p(Y)	0.000	0.360
		Ψ(NM)ϒ(NM)ε(NM)p(Y)	1.569	0.343
Grey fantail	*Rhipidura albiscapa*	Ψ(PT)ϒ(TC+NM)ε(YN)p(Y)	0.000	0.216
		Ψ(PT)ϒ(TC+NM)ε(.)p(Y)	0.291	0.207
		Ψ(PT)ϒ(TC+NM)ε(PT)p(Y)	0.849	0.220

Grey shrike-thrush	*Colluricincla harmonica*	Ψ(TC)ϒ(TC+NM)ε(TC+NM)p(YN)	0.000	0.372
Jacky winter	*Microeca fascinans*	Ψ(TC)ϒ(PT+NM)ε(PT+NM)p(Y)	0.000	0.336
		Ψ(TC)ϒ(PT+NM)ε(.)p(Y)	1.475	0.311
Laughing kookaburra	*Dacelo novaeguineae*	Ψ(PT)ϒ(TC)ε(PT)p(.)	0.000	0.235
		Ψ(PT)ϒ(TC+NM)ε(PT)p(.)	0.477	0.241
Little friarbird	*Philemon citreogularis*	Ψ(NM)ϒ(TC+NM)ε(PT)p(Y)	0.000	0.278
Magpie-lark	*Grallina cyanoleuca*	Ψ(.)ϒ(ITC+NM)ε(PT)p(Y)	0.000	0.169
		Ψ(.)ϒ(NM)ε(PT)p(Y)	0.127	0.160
		Ψ(.)ϒ(TC+NM)ε(PT)p(Y)	1.949	0.161
Mistletoebird	*Dicaeum hirundinaceum*	Ψ(.)ϒ(PT+NM)ε(PT+NM)p(YN)	0.000	0.342
		Ψ(.)ϒ(.)ε(PT+NM)p(YN)	1.757	0.316
Noisy friarbird	*Philemon corniculatus*	Ψ(.)ϒ(PT+NM)ε(.)p(Y)	0.000	0.262
		Ψ(.)ϒ(PT+NM)ε()p(Y)	0.000	0.262
		Ψ(.)ϒ(PT+NM)ε(YN)p(Y)	1.986	0.262
Noisy miner	*Manorina melanocephala*	Ψ(.)ϒ(YN)ε(PT+NM)p(Y)	0.000	0.810
Peaceful dove	*Geopelia striata*	Ψ(NM)ϒ(TC+NM)ε(PT)p(Y)	0.000	0.269
Pied currawong	*Strepera graculina*	Ψ(TC)ϒ(.)ε(PT+NM)p(YN)	0.000	0.173
		Ψ(TC)ϒ(PT)ε(TC+NM)p(YN)	0.404	0.182
		Ψ(TC)ϒ(PT+NM)ε(yearn)p(YN)	0.466	0.182
		Ψ(TC)ϒ(PT)ε(NM)p(YN)	0.760	0.169
		Ψ(TC)ϒ(TC+NM)ε(PT)p(YN)	0.892	0.179
		Ψ(TC)ϒ(PT+NM)ε(.)p(YN)	1.598	0.165
		Ψ(TC)ϒ(PT+NM)ε(PT+NM)p(YN)	1.820	0.196
Rainbow bee-eater	*Merops ornatus*	Ψ(NM)ϒ(PT+NM)ε(yearn)p(YN)	0.000	0.144
		Ψ(NM)ϒ(ITC+NM)ε(yearn)p(YN)	1.827	0.128
		Ψ(NM)ϒ(NM)ε(yearn)p(YN)	1.877	0.119
Red-capped robin	*Petroica goodenovii*	Ψ(PT)ϒ(.)ε(TC+NM)p(Y)	0.000	0.338
		Ψ(PT)ϒ(.)ε(NM)p(Y)	0.842	0.328
		Ψ(PT)ϒ(.)ε(TC)p(Y)	1.606	0.326
Red-rumped parrot	*Psephotus haematonotus*	Ψ(NM)ϒ(yearn)ε(ITC+NM)p(Y)	0.000	0.258
		Ψ(NM)ϒ(yearn)ε(ITC)p(Y)	0.875	0.247
		Ψ(NM)ϒ(.)ε(ITC+NM)p(Y)	0.882	0.247
		Ψ(NM)ϒ(PT)ε(ITC+NM)p(Y)	1.382	0.260
		Ψ(NM)ϒ(.)ε(ITC)p(Y)	1.840	0.236
Red wattlebird	*Anthochaera carunculata*	Ψ(NM)ϒ(TC+NM)ε(PT)p(Y)	0.000	0.479
Restless flycatcher	*Myiagra inquieta*	Ψ(TC)ϒ(PT+NM)ε(YN)p(Y)	0.000	0.327
		Ψ(TC)ϒ(TC+NM)ε(PT)p(Y)	0.051	0.327
		Ψ(TC)ϒ(PT+NM)ε(.)p(Y)	0.084	0.320
Rufous songlark*	*Cincloramphus mathewsi*	Ψ(NM)ϒ(NM)ε(NM)p(Y)	0.000	0.671
		Ψ(NM)ϒ(PT+NM)ε(PT+NM)p(Y)	1.343	0.682
Rufous whistler	*Pachycephala rufiventris*	Ψ(TC)ϒ(TC+NM)ε(PT)p(.)	0.000	0.270
Superb fairy-wren	*Malurus cyaneus*	Ψ(PT)ϒ(yearn)ε(PT+NM)p(Y)	0.000	0.509
		Ψ(PT)ϒ(PT+NM)ε(PT+NM)p(Y)	1.358	0.515
Superb parrot	*Polytelis swainsonii*	Ψ(NM)ϒ(PT)ε(PT)p(Y)	0.000	0.197
		Ψ(NM)ϒ(TC)ε(PT)p(Y)	1.006	0.185
		Ψ(NM)ϒ(PT+NM)ε(PT+NM)p(Y)	1.951	0.205

White-browed woodswallow	*Artamus superciliosus*	Ψ(NM)ϒ(TC+NM)ε(TC+NM)p(Y)	0.000	0.500
		Ψ(NM)ϒ(NM)ε(TC)p(Y)	1.288	0.487
White-plumed honeyeater*	*Lichenostomus penicillatus*	Ψ(NM)ϒ(TC+NM)ε(TC+NM)p(Y)	0.000	0.714
White-winged chough	*Corcorax melanorhamphos*	Ψ(PT)ϒ(ITC+TC)ε(TC)p(.)	0.000	0.220
		Ψ(PT)ϒ(ITC+TC)ε(.)p(.)	0.108	0.211
		Ψ(PT)ϒ(TC)ε(TC)p(.)	0.189	0.211
		Ψ(PT)ϒ(TC)ε(.)p(.)	0.376	0.203
		Ψ(PT)ϒ(TC)ε(PT)p(.)	0.633	0.217
		Ψ(PT)ϒ(ITC+TC)ε(ITC+TC)p(.)	1.043	0.223
		Ψ(PT)ϒ(TC)ε(NM)p(.)	1.445	0.206
		Ψ(PT)ϒ(TC+NM)ε(.)p(.)	1.579	0.206
		Ψ(PT)ϒ(TC)ε(ITC+TC)p(.)	1.785	0.213
White-winged triller	*Lalage sueurii*	Ψ(TC)ϒ(YN)ε(PT+NM)p(Y)	0.000	0.516
Willie wagtail	*Rhipidura leucophrys*	Ψ(NM)ϒ(NM)ε(NM)p(Y)	0.000	0.386
		Ψ(NM)ϒ(TC+NM)ε(TC+NM)p(Y)	0.003	0.398
Yellow-rumped thornbill	*Acanthiza chrysorrhoa*	Ψ(PT)ϒ(YN)ε(PT)p(Y)	0.000	0.284
		Ψ(PT)ϒ(YN)ε(PT+NM)p(Y)	1.340	0.287
		Ψ(PT)ϒ(NM)ε(PT)p(Y)	1.816	0.278
Yellow thornbill	*Acanthiza nana*	Ψ(.)ϒ(PT+NM)ε(PT+NM)p(Y)	0.000	0.240
		Ψ(.)ϒ(PT+NM)ε(.)p(Y)	0.864	0.213
		Ψ(.)ϒ(PT+NM)ε()p(Y)	0.864	0.213
		Ψ(.)ϒ(PT)ε(PT)p(Y)	1.579	0.218

614

615



616

617 Fig. 1. Map of the study area (south-west slopes, New South Wales, Australia) with sampling sites.

618

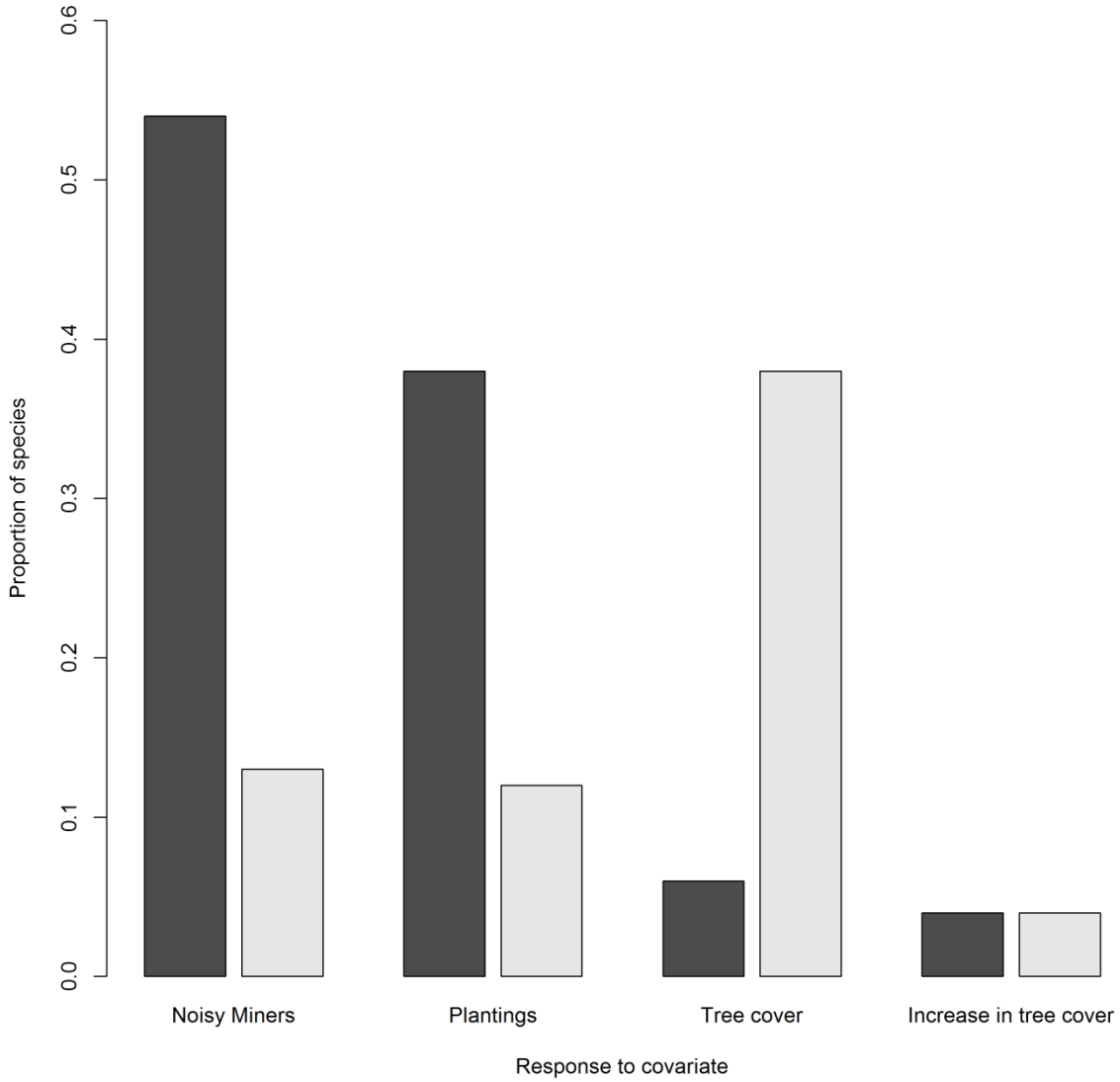
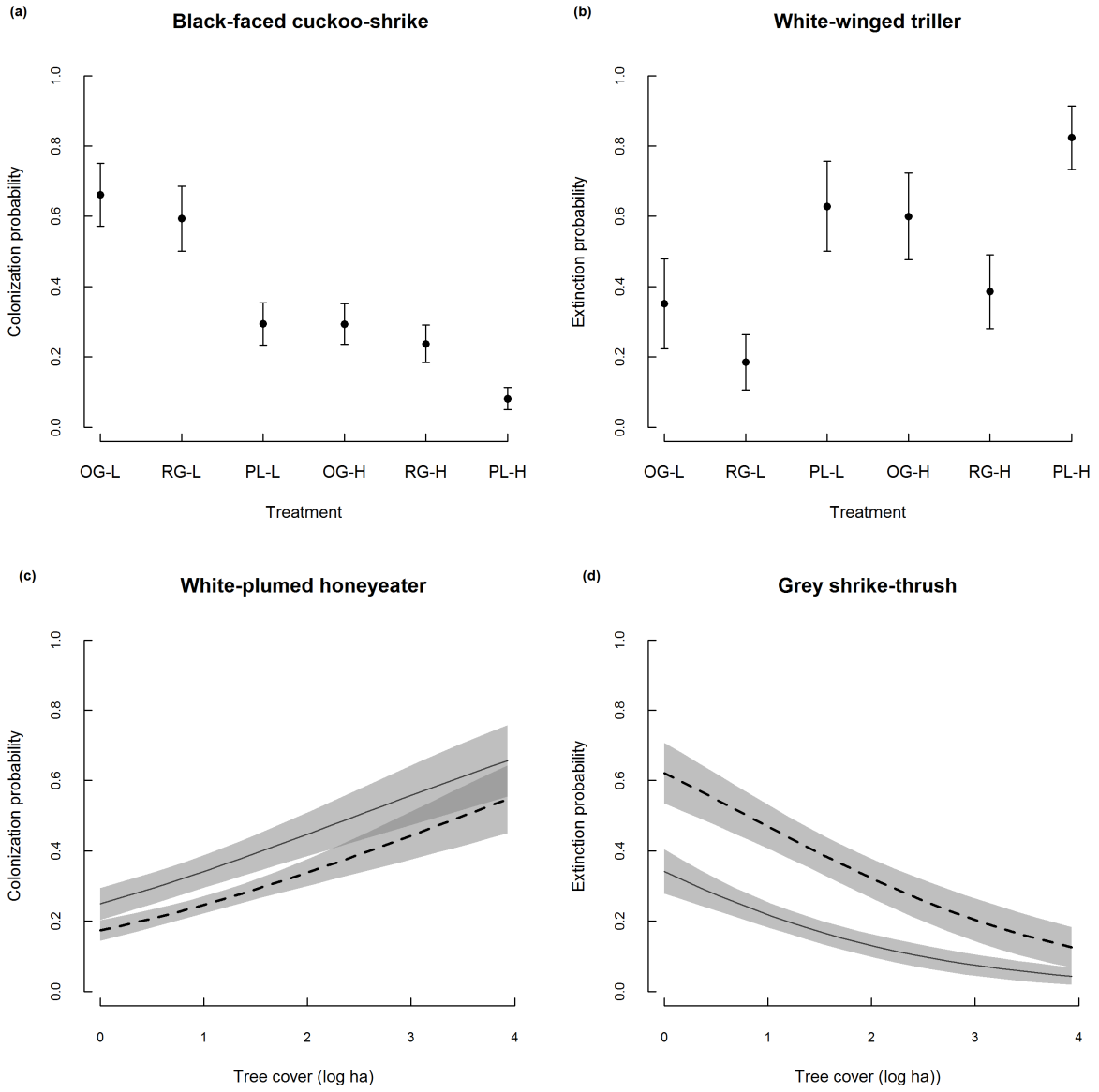


Fig. 2. Summary of the relationships between colonization/extinction rates and predictor variables (N= 42 bird species). Dark bars represent the proportion of species showing a negative relationship with the predictor variable (i.e. negative response implied either a decrease in colonization and/or an increase in extinction in response to a given predictor variable) whereas light bars represent the proportion of species showing a positive relationship with the predictor variable. Noisy miners= maximum abundance of noisy miners in a site, Plantings= response in relation to the old growth reference category, Tree cover= tree cover in the 78.5 ha circle surrounding each site, Increase in tree cover= increase in tree cover in the years preceding the survey as detected from Landsat images.

631



632

633 Fig. 3. Colonization and extinction probabilities (including SE) based on model averaged estimates of
634 top ranking models (ΔAIC < 2) for four example species. Panels (a) and (b) show two examples of a
635 response to noisy miners and patch type whereas (c) and (d) show two examples of a response to
636 noisy miners and tree cover (log hectares). In all four cases we made predictions using the 1st and
637 3rd quartile of noisy miner abundance (0 and 3 respectively). Predictions with 1st quartile are
638 labelled as L above and dashed line below, whereas predictions with 3rd quartile are labelled as H
639 above and continuous line below. OG=old growth, RG=regrowth, PL= plantings.

640